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WHY ARE FEMALE BIRDS OF PREY LARGER THAN MALES?

by

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For every complex problem there is a simple answer and it is wrong.

H. L. Mencken

The males of most birds are larger than the females, but the opposite is true of birds of prey—the hawks and owls of the orders Falconiformes and Strigiformes. In these females are, with few exceptions, larger than males—sometimes markedly so. These two orders are only distantly related, and one may assume that this reversed sexual dimorphism evolved independently in the two orders. Further, in the predatory family Stercorariidae, the skuas and jaegers (hunters), the female is also the larger sex; this family is related to the gulls (Laridae), not to hawks or owls.¹

In all these raptorial birds the claws of the feet are modified into curved, pointed talons, which are employed to seize, kill, or aid in killing the prey upon which they feed. In another somewhat predatory family, the Laniidae or shrikes, the bill is hooked as in raptors, but the claws are not modified into talons. The sizes of the sexes are not reversed in shrikes.

There are hundreds, indeed thousands, of other species of birds ranging from flycatchers and swallows to storks which are also “carnivorous,” and yet in which the male is the larger sex. But these species, with only occasional or rare exceptions, capture inoffensive prey—often insects, snails, and the like. Though predators in the literal sense, unlike the truly rapacious birds of prey, they do not have to subdue, kill, and rend their prey; and they have not evolved the hooked beak and talons—or the fierce disposition that goes with such weaponry.

To analyze in detail the data supporting reversed sexual dimorphism in raptors and the possible explanations for it would require a volume. Here the intention is merely to summarize some of the hypotheses that have been advanced and to evaluate them briefly. Neither have I presented in detail the raw data which may be found in various reference works. It may be noted, however, that there is a need for further quantitative data on size dimorphism in raptors. This is particularly true of weights, which reflect the dimorphism better than do linear measurements, such as wing length. The family Stercorariidae illustrates this point. Linear measurements often show superiority in size of the female in the skuas (*Catharacta*) but not in the smaller jaegers (*Stercorarius*) (see, for example, Ridgway, 1919:681-695). When, however, adequate samples of weights of the three species of jaegers were assembled (Maher, 1974:11-12), it became evident that females are appreciably heavier than males in this genus also. Or, as another example, the wing length of the male American Goshawk (*Accipiter gentilis atricapillus*) averages about 97 percent of that of the female; it weighs a full 20 percent less.

¹ In the frigate-birds (*Fregatidae*) females are larger than males. Since these birds are somewhat predatory, it has been assumed (Amadon, 1959) that this is another example of sexual size reversal in raptorial birds. Perhaps so, but the fact that the same is true of the related fish-eating boobies (*Sulidae*) but not of the cormorants (*Phalacrocoracidae*) makes it possible, if not likely, that other selective factors are at work in this order (*Pelecaniformes*).

In their analysis of size dimorphism in North American owls Earhart and Johnson (1970) couch the discussion of weight largely in terms of the cube root of that dimension. This converts weight to a statistic comparable with linear measurements, such as wing length. Still, it is worth emphasizing that selection for body size results from the actual weight or mass of the bird. The authors mentioned take this for granted in their discussion of the sexual difference in wing loading that results from dimorphism in size.

Variation in Degree of Dimorphism

Raptors vary greatly from genus to genus and sometimes from species to species in the amount of sexual size dimorphism. Those species that are most rapacious and kill the largest prey relative to their own size have the greatest dimorphism. Examples range from certain eagles, such as the Black and White Hawk-eagle (*Spizastur melanoleucus*), the horned and eagle owls (*Bubo*), and the larger falcons (*Falco*) to small species of *Accipiter* and some small owls. In many of these the male is a full third smaller than his mate, and hence called a "tiercel" by falconers. In a few species of *Accipiter* the male weighs only about half as much as the female.

Birds of prey with the propensity to attack large and at times dangerous prey committantly develop the fierce and aggressive disposition necessary for such foraging. In species that take smaller or humbler prey, such as rodents, fish, and lizards, sexual dimorphism is less, but often still substantial. For example, in sea-eagles (*Haliaeetus*), various species of *Buteo*, and others the weight of males may average one-fifth to one-fourth less than that of females. In primarily insect- and snail-eating raptors, or those that are in part scavengers, such as caracaras (*Polyborus*) or some kites (*Milvus*), size dimorphism is usually even less and may be negligible.

The social habits of certain kites may also have ameliorated their aggressiveness and led to an abatement in selection for sexual dimorphism. The same may be true of Eleanor's Falcon (*Falco eleanorae*), which, as Dr. Noel Snyder (in litt.) has pointed out to me, shows remarkably little dimorphism for a bird-eating species. To be sure, the fact that most of the birds it catches are small may be a factor. Social habits and extensive use of insects as food may explain the fact that in the Burrowing Owl (*Athene cunicularia*) males average slightly larger than females.

Another exception is the Secretary-bird (*Sagittarius serpentarius*); it occasionally kills large, venomous snakes, but its claws are blunt, not modified into talons. Though classified with the birds of prey, it may be unrelated to them. Among vultures, which are for the most part entirely carrion eaters, the sexes are of about the same size, or the male may even be a little larger. The claws of vultures are long, coarse, and blunt—no longer talons. The Old World vultures, in particular, are closely related to other birds of prey and presumably derived from them. It is reasonable to assume that as they gradually lost their predatory habits, they also lost their reversed sexual size dimorphism.

The correlation just traced is sometimes evident among the species of a single genus. The Peregrine Falcon (*Falco peregrinus*) preys on birds, including large ones; it has pronounced dimorphism. More or less insectivorous species of the genus, such as the kestrels, are less dimorphic. Bird-eating species of *Accipiter* are highly dimorphic; the amphibian-eating Grey Frog-hawk (*A. soloensis*) of the Orient is less so. Earhart and Johnson (1970:260) found that within a single species, the Screech Owl (*Otus asio*), the chiefly insectivorous subspecies are less dimorphic than ones that take many birds and small mammals. The same may be true of the American Kestrel (*Falco sparverius*) (Storer, 1966:433-434).

Thus, one finds on the whole a remarkably close correlation in birds of prey between degree of rapaciousness and degree of reversed sexual dimorphism.

Why Reversed Dimorphism?

Hypotheses fall into two main categories. The first relates reversed sexual dimorphism to one or another aspect of reproductive behavior. I continue to favor one such hypothesis. But before discussing behavioral explanations, I shall consider and attempt to dispose of the prevailing alternative hypothesis, namely, that dimorphism in raptorial birds is an adaptation to widen the food niche.

That is, if the larger female takes larger prey on the average, and the smaller male takes smaller prey, between them they will utilize a greater diversity of the potentially available food. Such expansion of the food niche might be important during the nesting season, when the pair of raptors is restricted to the general vicinity of the nest and when they have voracious young to feed. It might also be of importance to some species during winter or other periods of possible shortage of food.

At present those who see in the size dimorphism of raptors an adaptation to expand the food niche are in the majority. This may be attributed in part to the current popularity of studies embraced by such terms as "time and energy budgets," "(avian) energetics," "adaptive strategies," and "physiological ecology."

There are certainly birds and mammals in which the sexes differ in size but eat the same thing (e.g., grazers, whether geese or wild cattle). Among predators, however, as would be expected, large individuals tend to kill larger prey than do smaller ones. Large female accipiters take on average larger prey than do the smaller males (Storer, 1966; Brosset, 1973), and the same is true of *Circus* (Schipper, 1973) and doubtless of other highly dimorphic species, such as the larger falcons.

But the fact that a large hawk (or person) eats more and prefers larger bites than a smaller one is not necessarily the reason it is larger.

Reasons for doubting the ecological or niche-expansion explanation of reversed sexual size dimorphism among raptorial birds are the following:

First, as already summarized, the degree of sexual dimorphism in raptors is correlated with the relative size of the prey taken, not with the potential of the food supply for supporting dimorphism. Species that regularly or not infrequently attack and kill birds or mammals as large or larger than themselves have the greatest dimorphism. Such species range in size from sparrow-hawks to big eagles. Species that take humbler prey, even when there would seem to be as great or greater potential for broadening the food niche, are less dimorphic.

Second, the ecological hypothesis fails to explain, at least convincingly, why it is the female that is the larger sex. Some (e.g., Selander, 1966:139) recognize this failure and attribute the initial impetus towards reversal to behavioral factors, but then assume that the dimorphism, because of its extent, must be under ecological control. Others have suggested (Prof. E. Mayr, pers. comm.) that since the male does most or all of the hunting in the first half or three-fourths of the nesting cycle, it is advantageous for it to be the smaller sex because (a) there are more species and individuals of small than of large prey (Elton's "pyramid of numbers"), and so the male can get more food at the time he is doing all the hunting; and (b) smaller prey is more suited to the chicks when they are small.

There are a number of caveats to be entered here. Will a larger number of small prey always add up to a larger biomass, especially when much of the prey has to be transported to the nest? Some buteos feed on insects when away from the nest but carry only vertebrates to the nest; insects are too small to make it worthwhile. Certain species commence nesting when the country is still cold or even snowbound, when the prey animals have not yet brought forth their young, and when smaller rodents are less available. The strongly dimorphic Great Horned Owl (*Bubo virginianus*) in the northern parts of its range begins nesting in late winter when the ground is still covered with snow. Not until weeks later, when the young are well grown and when the female is also hunting, are young prey animals

available. Nor is small prey necessarily more suited to the chicks. The female might find it easier to tear bits of flesh for the young from, say, a rabbit, than from a mouse.

Dr. Ned Johnson (pers. comm.) has suggested to me that following an initial selection for larger size in the female for behavioral reasons, females that paired with smaller, more agile males that were better foragers would leave the most progeny. Skill in aerial food passing in courtship might be part of such selection. This hypothesis is attractive for such species as harriers (*Circus*) or some falcons, but if one considers it in the gamut from small owls to eagles it is less convincing. A raptor that is a little less agile may offset it by catching bigger prey. The larger female does some effective hunting after the young are well grown, as well as hunting for herself during the nonbreeding season.

Reynolds (1972) concluded that if dimorphism is an adaptation to broaden the food niche, then it will be greatest in bird-catching species, such as the Sharp-shinned Hawk (*Accipiter striatus*), in which the size of the predator approximates that of the agile prey. But surely the vast majority of the birds caught by this species and by related ones, such as the European Sparrow-hawk (*A. nisus*), weigh no more than a third or perhaps half as much as the hawk. The argument is perhaps undercut to some extent by Reynolds's evidence that the larger female, when she does commence hunting later in the cycle, is effective because her size enables her to take a greater size range of prey. And as with other ecological hypotheses, the pronounced dimorphism in many species that catch few birds remains unexplained. Weight data (Glutz, Bauer, and Bezzel, 1971:173,642) indicate, for example, that in the European race of the Golden Eagle (*Aquila chrysaetos*) and even in the White-tailed Sea-eagle (*Haliaeetus albicilla*) the average weight of the males is a full 25 percent less than that of the females.

Third, a survey of the animal kingdom suggests that sexual dimorphism in size is usually correlated with mating behavior (Amadon, 1959). In general, males are more aggressive than females; they compete for mates. Larger and stronger males have an advantage in perpetuating their genes. This distinction may be less apparent in birds than in mammals, but it exists. Even in the occasional insect in which males contest physically for mates, selection has produced larger size in that sex (Beebe, 1947). The increased dimorphism often found in polygynous or promiscuous species, such as some of the larger grouse (*Tetraonidae*) or pheasants (*Phasianidae*) or bustards (*Otididae*), further illustrates the point. In highly polygynous seals (Phocidae), such as the elephant-seals (*Mirounga*) or northern fur seal (*Callo-rhinus*), two genera that are not closely related, males weigh several times as much as the females. In these polygynous birds and mammals, males are to a degree expendable; only a few are needed for fertilization. Hence, sexual dimorphism can proceed further than in monogamous species. In the latter, among seals as well as birds, dimorphism is much less. An ecologist who saw in the enormous dimorphism of some of the polygynous seals an adaptation to broaden the food niche would surely be mistaken!

When the parental-care role is reversed, as in phalaropes (*Phalaropidae*) or button-quail (*Turnicidae*), and the males incubate and care for the chicks while the females compete for mates, it is the females that are the larger, and, when there is a distinction, the more brightly colored sex. Female button-quail are so pugnacious that they are pitted like miniature gamecocks. The reversed sexual dimorphism of raptors is not associated with reversed roles in parental care. The instances above are merely cited to further illustrate the responsiveness of size to selection by reproductive behavior.

The skuas and jaegers (*Stercorariidae*) seem to confirm this observation. In the related gulls (*Laridae*) males are larger than females. Yet, when the skuas became even more predatory than gulls, and, especially, one supposes, when they developed small, curved "talons" that could pose a threat to the female in pairing and territorial encounters, selection came to favor larger size in the female. Perdeck (1960), who studied nesting behavior in

the Great Skua (*Catharacta skua*), is quoted on this point below.

Though probably without immediate relevance to the situation in birds of prey, one may cite Jehl's (1970) study of dimorphism in certain Scolopacidae. In the Stilt Sandpiper (*Micropalama himantopus*) and the Least Sandpiper (*Erolia minutilla*) he found that individually small males and large females pair first and are most successful in nesting. Again, if he is correct, the dimorphism has its basis in reproductive behavior, not in ecology. The fact that the female is the larger sex in these shorebirds is unrelated to the situation in raptors, but reflects the trend towards reversal of parental care in shorebirds that has become complete in such groups as the phalaropes.

Thus there is varied evidence that sexual size dimorphism among higher animals is commonly the result of patterns of mating behavior. The burden of proof is upon those who suggest that the same is not true of raptorial birds.

Fourth, there are doubts as to the theoretical basis of the ecological or niche-expansion theory. One assumes that intraspecific competition among birds is regulated by such adaptations as territory, peck order, delayed reproduction, cannibalism, and the like. Such competition is often density dependent and will not lead to extinction. Interspecific competition, on the other hand, may pose a direct threat to survival, and thousands of species have doubtless succumbed to it—sometimes, to be sure, when also beset by environmental changes. Because the environment does change seasonally, annually, and over longer periods, successful species evolve various safety factors. One may be a body size that is not rigidly limited by food or environment. Such ecological amplitude may be especially necessary in top-level predators whose food supply is often more uncertain and fluctuating than that of the grass eaters which sustain them.

Hence in species in which mating behavior makes sexual dimorphism in size advantageous (and this includes most birds and mammals), the ecological niche, one supposes, is often or perhaps usually molded by selection to accommodate the size variation and not vice versa. Such modifications may entail increased size of territory, heightened interspecific aggression, etc. Some species, to be sure, adjust with difficulty; perhaps this is why certain raptors, such as the Ayres' Hawk-eagle (*Hieraetus dubius*) or the Taita Falcon (*Falco fasciunucha*), are so rare. Others become extinct.

To state this the other way around, would not interspecific competition be least when a species is clustered around its optimal competitive size, without sexual-size dimorphism? If so, the widespread occurrence of dimorphism among higher animals may be regarded as a behavioral necessity. To what extent theoreticians have dealt with such questions I do not know. Schoener's contributions (e.g., 1968, 1969a, 1969b) seem to deal with rather complex situations, and his equations have so many variables as to render conclusions from them tentative.

Even if interspecific competition is disregarded, sexual differentiation in food or foraging niche may not be advantageous in the long run. If the food supply changes, there are two things that can go wrong, not one. It may be more difficult for such a dimorphic species to adjust to changing food resources or levels of interspecific competition.

Thus when it is demonstrated that the smaller male, as might be expected, requires fewer calories than does the female (Mosher and Matray, 1973) of the Broad-winged Hawk (*Buteo platypterus*), one does not need to accept the suggestion that the smaller size of the male reflects direct selection to lessen caloric requirements. Why would such selection have affected the male only? Why do species become larger in the first place if caloric requirements are of such crucial importance? This, of course, is not to deny the importance of such studies in determining physiological parameters.

The fossil record contains many examples (and in diverse groups!) of a trend towards increasing size. Larger individuals may secure more mates, or they may be able to shoulder companions away from food or other necessities (Simpson, 1944:86). The trend towards larger size is a general one, and the blue whale (*Balaenoptera musculus*), a plankton eater, has become the largest known animal of all time. In thousands of diverse animals, and perhaps one might include plants, size has not been so rigidly controlled by food or other environmental factors as to preclude gradual change. Often it has continued to change over vast periods of time.

To be sure, a number of examples of sexual dimorphism in birds apparently represent adaptations to expand the available food resources (summarized by Selander, 1966). These usually relate to the primary food-gathering organ, the bill, rather than to general size, and the species concerned are chiefly inhabitants of depauperate islands where interspecific competition will usually be less than on continents. Even so, the evidence that the observed sexual differences in foraging are the *cause* of the dimorphism is circumstantial. Perhaps the species-poor habitats merely provide more scope for divergence resulting from social or sexual behavior (dominance, peck order, mating systems, facilitation of sex recognition, etc.).

I do not, of course, wish to deny that food availability or lack of availability may sometimes have had something to do with degree of dimorphism in raptorial birds. Earhart and Johnson (1970) found some races of *Bubo virginianus* to be slightly more dimorphic than others; this may reflect some environmental influence, but it could be a result of mere chance.

Behavioral Explanations

It will be clear from what has preceded that I continue (Brown and Amadon, 1968:26-28) to think that the explanation for the reversed sexual size dimorphism of raptorial birds is to be sought in the relationships of the male and female at the time of pair formation and perhaps throughout the reproductive period. Before discussing this, we may dispose of hypotheses based on other aspects of behavior.

First, it has been suggested that male birds of prey, lacking "maternal" instincts and accustomed to killing small animals, may pose a threat to the life of nestlings. Selection might then favor larger size in the female so that she can prevent any such attempts by the male. Perhaps such reflections were influenced by knowledge of certain mammals, such as cats and bears, in which the males are, in fact, a threat to the young. There is now ample evidence that even in raptors with pronounced sexual dimorphism the male often incubates to some extent and may even have a brood patch. He sometimes feeds the chicks and certainly poses no threat to them.

A second hypothesis suggests that selection has favored larger size in the female raptor, the better to enable her to protect the nest and its contents from predators of other species. This suggestion is more difficult to disprove, but I do not think it will pass muster. It is true that the female spends more time at the nest than the male, but why, if nest defense explains the larger size of female raptors, should the dimorphism be greatest in fierce species that catch relatively large prey? It might be argued that because they are fiercer, they defend the nest more vigorously; therefore selection for increased size is more severe. This is rather tenuous reasoning. To be sure, two fierce species, the Great Horned Owl and the Goshawk, are the North American raptors that most often attack humans climbing to the nest. But it is also true that many raptors with rather pronounced dimorphism, such as the two species of North American eagles, are lackadaisical about nest defense, at least insofar as humans are concerned.

Scattered evidence indicates that males do participate in nest defense. In Great Horned Owls both members of a pair sometimes attack an intruder, striking alternate blows. Both members of a pair of Ferruginous Hawks (*Buteo regalis*) attacked a coyote that was unsuspectingly approaching their hillside nest (Angell, 1969). A male Merlin (*Falco columbarius*) sometimes appears, screaming in protest, when an intruder is still far from the nest. When raptors nest or attempt to nest in captivity, both members of the pair may become very aggressive towards man or any intruder, as was true of an observed pair of Harpy Eagles (*Harpia harpyja*) (Dr. William G. Conway, pers. comm.).

Nest defense is a two-edged sword: better to flee and live to nest another day than to be killed by a nest predator. Golden Eagles occasionally bring Great Horned Owls to their young as food; perhaps these were owls that defended their own nests too vigorously! The species of raptors found in any particular area usually exhibit wide divergence in dimorphism; it seems unlikely that nest defense is more important to some of them than to others.

Thirdly, the suggestion is made that contests between male raptors are primarily brilliant aerial maneuvers and that smaller size in the male, far from being a handicap, is an asset. This is an attractive idea as applied to a dashing falcon, but not for a big eagle or a horned owl. Further, Cade (1960) found that large falcons do in fact make bodily contact in aerial encounters and that sheer physical prowess is the deciding factor.

We turn, finally, to the hypothesis that reversed sexual dimorphism is the result of reproductive interactions between the sexes. Pair formation may prove to be the decisive phase.

In highly dimorphic birds as regards color—many pheasants, for example—sex recognition may be innate; but in the numerous species in which the sexes are externally alike, and this includes most raptors, initial pair formation is often—as the late R. C. Murphy once put it—a matter of trial and error. Typically, the male takes up a territory and, by displays and vocalizations, warns off other males and attracts females. He is hostile to *any* approaching conspecific, treating it as a potential rival and buffeting it or otherwise seeking to chase it away. If the approaching bird is a female prepared to mate, she behaves submissively, refuses to be repelled, or thereafter returns and a pair is formed (Lack, 1940).

If this is the sequence in raptors, and many more observations are needed, may not the female be in actual peril from a male armed with talons and (judging from birds in general) innately more aggressive than she? Indeed, the male might first appraise an approaching bird of his own or smaller size as potential prey! In such species selection would, one assumes, have favored females that were as large as, or eventually larger than, the male so that despite their somewhat more submissive or passive nature at the time of pairing, they would not be intimidated or imperiled by the male. This would be especially true of species that unhesitatingly attack birds as large or larger than themselves. It is in such species, as has been already emphasized, that the superior size of the female is usually most pronounced.

If such is the case, one might ask why sexual dimorphism is substantial in some buteos, fish eagles, and the like, which subsist on rather humble prey. These raptors are, however, all armed with dangerous talons, and most of them do at times attack large birds or mammals. A few examples will be given. A Red-tailed Hawk (*Buteo jamaicensis*) when flushed, flew off carrying the body of one of its own species which it had apparently killed and was eating (Clevenger and Roest, 1974). A White Hawk (*Leucopternis albicollis*), a species that normally feeds on small snakes and the like, killed a tinamou (*Tinamus major*), a bird that would weigh more than the hawk (Lamm, 1974). The American Kestrel occasionally tackles a bird as heavy as itself. The Bald Eagle (*Haliaeetus leucocephalus*), though partial to fish, not

infrequently pursues and kills large birds; some individual eagles do so habitually. Further, *Accipiter* and *Falco*, instructive though they may be, do not provide all the necessary evidence. For example, speculation about the correlation of increased sexual dimorphism in color and reduced dimorphism in size in *Falco sparverius* cannot ignore other genera (or even other species of kestrels) in which no such color dimorphism exists.

Careful observations of both wild and captive raptors are needed. The behavior of captive birds may be significant but must be interpreted with caution. In the wild, for example, courtship or pairing flights may cover miles of terrain. Willoughby and Cade (1964) in an attempt to study dominance in relation to size dimorphism, paired a male of the northern race of *Falco sparverius* with the female of the smaller southern subspecies, thereby forming a pair of about the same size. Behavior did not seem abnormal, but this is a species of rather moderate dimorphism.

It might be argued that things have swung too far. In courtship feeding in the Peregrine Falcon the male sometimes appears terrified of the larger female; she snatches the prey from his grasp as he speeds by. Where attempts have been made to breed various species of *Accipiter* in captivity, the male, lacking sufficient room to flee, is sometimes killed by the female. Nonetheless, under natural conditions, one assumes that the existing degree of dimorphism in each species is the optimum under existing selection pressures.

As noted earlier, Perdeck (1960:129) in his study of *Catharacta skua* came to the conclusion set forth above as to the reason for reversed sexual dimorphism. If he was correct, the same could be true of hawks and owls. He summarized as follows (slightly paraphrased):

Perhaps the piratical and sometimes predatory habits of the skua have something to do with the reversed male-female size ratio, as compared with the gulls. A predatory bird needs a high aggressiveness towards other birds that may not only be its equal in size but also be of the same general appearance (skuas prey upon gulls). But this extreme aggressiveness is a drawback in pair formation and mating. A male has to perform the most 'aggressive' part of the mating. For the male to be in general more aggressive than the female has, therefore, survival value. But he must, of course, not be too aggressive! The chance of this occurring is greater in a species that, because of its feeding habits, requires an extra 'dose' of aggressiveness. For such a species a reduction in the size of the male relative to that of the female may have survival value.

In passing, it may be noted that sex recognition in predatory mammals is based on other cues, probably initially olfactory ones, and there is no reversed dimorphism.

To attribute such a fundamental character as sexual dimorphism in size in raptors to a selective pressure that operates only during the relatively brief period of pair formation and mating may seem unrealistic. Yet many birds (and mammals) are encumbered throughout adult life with "ornaments" used only at that season (for example peacocks [*Pavo*]). At the same time it is possible that the reversed dimorphism of raptors may enhance reproductive success throughout the entire nesting cycle. Cade (1960) wrote as follows:

A reproductively successful pair bond can result only when the female falcon is clearly dominant to the male . . . and when the male makes a biologically adequate adjustment to his subordinate role in the pairing situation. . . . Female dominance appears to function in some as yet unknown way in holding the male to his role as food provider for the female and the young. . . . On the average, females that mate with males smaller than themselves were able [one supposes] to maintain better dominance relations, and more progeny of such pairs survived. . . . Even in Kestrels, in

which the dimorphism is less, the females "assert a vigorous dominance over their mates."

In the Goshawk, Schnell (1958:385) found that the female had a special cry with which she "dismissed" her mate; and she did not begin feeding the chicks until after he had left the vicinity of the nest. Kemp and Kemp (1975) observed a female Ovampo Sparrow-hawk (*Accipiter ovampensis*) threaten her mate when he remained at the nest after she had finished eating a prey item the male had brought. The male then left immediately. But there are hundreds of species of birds in which one sex, usually the female, assumes the entire duties of parental care without stimulus or assistance from the mate. There are a few observations of male hawks that continued to feed the chicks after the death of the female, and there is no real evidence that physical (or sexual) dominance by the larger female has anything to do with the fact that her mate hunts for her and for the chicks.

How may one demonstrate conclusively whether behavioral or ecological factors or both led to reversed sexual dimorphism in raptorial birds? Comparison of the degree of dimorphism with the opportunities for ecological expansion might provide clues, e.g. comparison of the dimorphism and food resources of the subspecies of *Buteo jamaicensis* on the tiny island of Socorro off the Mexican coast with those of one of the mainland subspecies. Mating and parental behavior may be observed both in the wild and among the raptors that are being bred with greater success in captivity. The data acquired may prove difficult to interpret at least initially, but will also be valuable for other purposes.

I am grateful to Messrs. John Bull and Mark Fuller and the others who helped me with this paper.

Summary

In most birds of prey, including such unrelated ones as hawks (Falconiformes), owls (Strigiformes), and skuas (Stercorariidae, Charadriiformes), females are larger than males, sometimes substantially so. This reversed sexual size dimorphism in raptors is greatest in species that pursue, kill, and rend large, active prey; less in those that kill small rodents or insects; and absent or virtually so in vultures. In some species it has been shown, as would be expected, that the larger females catch on the average larger prey than the smaller males. Some ecologists conclude from this that the dimorphism is an adaptation to increase the total size range of prey available to a raptorial species. This hypothesis does not explain why the dimorphism is greatest in fierce species that kill large birds and mammals, why in some dimorphic species the sexes apparently take food of the same size, or why it is the female that is the larger sex, although an attempt has been made to correlate the last point mentioned with ecology.

Furthermore, in higher vertebrates in general, sexual dimorphism in size is correlated with mating behavior, not with foraging ecology; it is usually a result of competition by males for mates. When it is the females that compete for mates, then that sex is the larger. Although female raptors do not compete for mates, they are larger than the males; the explanation is probably still to be found in mating behavior. Raptors have become unusually aggressive birds, presumably because they hunt and kill active prey at some risk of injury to themselves. Furthermore the male, as in birds in general, may be expected to be the more aggressive sex, at least at the time of mating and pair formation. Armed as he is with formidable beak and talons, he would pose a threat to the physical well-being of the female during pair formation, which in birds involves aggression by the male during its earlier stages. To offset this, selection would favor greater physical prowess in the female, and hence that sex has become the larger one, especially in the most aggressive species.

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HARRIS' HAWK KILLS EGRET

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The Harris' Hawk (*Parabuteo unicinctus*), though it captures many small animals and is even said to take carrion, at times tackles larger prey without hesitation, both in the wild and when trained for hunting, as the following experience illustrates. On the morning of January 25, 1975, I was photographing in a swampy area along a road in San Luis Potosi, Mexico. A Harris' Hawk flew in, swooped on a lone nearby Snowy Egret (*Egretta thula*), and carried the squawking heron about one hundred yards to a low stub. When I approached, the hawk carried its prey about fifty yards further, landing in a palm tree and dropping the egret, still alive, at its base. Six other snowies flew around the victim excitedly, and then a Common Egret (*Casmerodius albus*) flew in and lit nearby for a couple of minutes. After ten minutes the hawk dropped down, seized the egret which was still able to squawk once or twice more, and laboriously carried it off behind a screen of trees, where the hawk apparently fed. A quarter of an hour later the hawk, unencumbered, returned to its perch in the palm. Probably the egret weighed about half as much as the hawk.

ECOLOGY AND REPRODUCTION OF RED-SHOULDERED HAWKS IN THE WATERLOO REGION, SOUTHERN ONTARIO

by

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Abstract

A study of *Buteo lineatus* was done in 1973 for the Canadian Wildlife Service in south-central Ontario. Six pairs were studied in the Waterloo Region for habitat requirements, behavior (especially breeding and feeding), interspecific competition, and reproductive success. In 1973 two (and perhaps three) pairs raised young, two deserted, and two outcomes were not definitely known. Other aspects of reproductive history were deduced from past notes and Ontario Nest Record Cards for the Waterloo Region and surrounding counties. A decline in nesting numbers was noted over a period of 10 years. Loss of habitat and prey, and increasing raptorial competition, seem to be causing a decline in this species. Three eggs were analyzed for residues of organochlorines and mercury. Eggshell thicknesses were also recorded. Thickness index was calculated for 70 eggshells from this area. A 14.5 percent decrease in eggshell thickness has occurred since 1947.

Introduction

Five races of Red-shouldered Hawks (*Buteo lineatus*) range extensively through temperate and subtropical North America. The northern subspecies (*B. l. lineatus*) has a wide breeding distribution in the hardwood and mixed forests of the Upper Austral/Carolinian-Transition/Alleghenian zones, barely onto the Canadian Shield. It was one of the most common raptors throughout this range. Southern Ontario is the principal Canadian nesting grounds of this subspecies; the lower Great Lakes mark the northern limit of its regular winter distribution.

Study Area and Methods

The Waterloo Region, in the center of southwestern Ontario, with its numerous well-watered valleys, rapid rate of urbanization, and high level of agriculture has long had a concentration of nesting Red-shouldered Hawks, despite a pronounced decline since the 1960s. Since 1953 I have observed nesting of this buteo in the Waterloo Region. During 1973 I studied six pairs as a pilot project for the Canadian Wildlife Service (CWS). The Red-shouldered Hawk has seldom been studied intensively except in Massachusetts (Kennard 1894), Maryland (Stewart, 1949; Henny et al., 1973), and Michigan (Craighead and Craighead, 1956). Henny (1972) gave a brief summary of its population dynamics, and Bent (1937) produced a full account of the northern race. Recently Hanna and Wiley (unpubl.) worked on Red-shouldered Hawks in Ontario and Florida respectively.

From 12 pairs of *B. lineatus* known to be present within the 528 sq mi (1368 sq km) of Waterloo Municipal Region (formerly County), 6 were chosen for study. They were selected on the basis of accessibility of nests and proximity to each other. Each pair was visited six to eight times in optimum weather during the 1973 reproductive season. Ecological conditions—especially habitat, interspecific competition, general behavior, and reproductive suc-

cess—were recorded. Unfortunately, only two nest trees could be climbed safely. (Earlier data at the Royal Ontario Museum, Toronto, were also consulted.)

My study sites varied from 970 to 1230 ft (295 to 375 m) above sea level. The average elevation of the region is 1000 ft (305 m). The study areas were settled between 1806 and 1853. Three nearby cities had populations ranging between 62,000 and 149,000. All study sites were in heavily glaciated and dissected topography near streams and/or ponds. Four occupied nests were located on urban plots: a golf course and relict woodlots. The other two were in farm woodlots within the urban shadow; one of these was adjacent to a subdivision.

All territories studied were in woods of Alleghenian or Transitional affinity, with principal hardwoods being beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*). The southernmost woods contained a considerable percentage of oak (*Quercus* sp.); only one wood was devoid of eastern hemlock (*Tsuga canadensis*).

Red-shouldered Hawk breeding territories range up to one square mile (2.59 sq km) in extent (Craighead and Craighead, 1956). An area of about that size around each nest was examined and mapped. Vegetation in a 0.10 ac (0.0405 ha) circular plot centered on the nest tree was further quantified for main types of cover following the method of James and Shugart (1970).

Pair 1

Pair 1 utilized the most urban territory, which generally represented the minimal habitat requirements in the study region. Construction and both residential and industrial traffic surrounded this pair throughout 1973, sometimes as near as 30 ft (9.1 m)! Even tree-cutting (to clear land for houses) and bulldozing (which altered drainage into a pond) did not deter them. Many salamanders and frogs continued to spawn in the shrunken woodland pool. These and snakes were hunted. Competition with other raptors was slight or nil.

The nest tree was well within a 36 ac (14.6 ha) mature deciduous wood. Forty-four trees having a diameter of 3 in (7.5 cm) or more occurred in the 0.10 ac sample plot with a total basal area of 22.3 sq ft. Ground cover was 80 percent; canopy cover, 65 percent. The nest tree was a slender high-crowned ash (*Fraxinus* sp.) with a DBH of 15 to 20 in (38.0 to 50.0 cm) and a height of 70 ft (21.3 m). The rather flimsy nest was at a height of 55 ft (16.7 m).

Pair 2

Pair 2 utilized a more secluded, but still urban, area. Active and derelict farming, construction of a multiple-dwelling subdivision, and golfing occurred nearby. Estate homes on wooded lots were the closest habitation. Below the nest was a spring-fed stream and a swampy depression that had almost dried up.

Food on the manicured golf course hardly seemed sufficient for the single pair of Red-tailed Hawks (*Buteo jamaicensis*) and the Great Horned Owls (*Bubo virginianus*) that nested there. I found no amphibians or reptiles in the area.

The Red-shouldered Hawk nest was 40 ft (12.2 m) up in a 64 ft (19.5 m) beech of 15 to 20 in DBH. It was on a hemlock-hardwood ridge within a broken, 88 ac (35.6 ha) tract of mature woods. Twenty-four trees having a DBH of 3 in or more were found in the 0.10 ac plot. Their combined basal area was 14.4 sq ft. The woods were being thinned, but ground cover was still 65 percent and canopy cover 95 percent.

Pair 3

Although well within a recently annexed area and within 120 ft (36.5 m) of a major arterial road, this territory was well buffered. Derelict farmland and a large abandoned

millpond, along with extensive reforestation across the highway, flanked the relict conifer-hardwood bush of 10 ac (4.0 ha) within which the nest was placed. Beyond these buffers subdivisions were being built near the old community of Doon.

Small birds, rodents, and amphibians were moderately plentiful; swales and a permanent nonchannelized but polluted creek were nearby.

The nest was 40 ft high, in a 60 ft (18.2 m) beech of 30 in (75.0 cm) DBH—one of the largest trees on the tract. Within the sampled plot were 58 trees having a DBH of 3 in or more; their total basal area was 23.8 sq ft. Ground cover was only 15 percent; canopy cover was 85 percent.

Pairs 4 and 5

Pairs 4 and 5 were on the extreme edges of cities. Largely intact swamps with some suburbs encroaching upon them provided favorable hunting grounds, but some lumbering occurred at both sites. Water sources were permanent and of good quality. Nesting was in upland mature mixed woods along ridges overlooking wide expanses. Nests were within forests of 10-40 ac (4.0-16.2 ha), in 55 to 60 ft beeches having a DBH of 21 to 27 in (52.5-68.0 cm).

Hikers passed near one site, and cattle grazed at the other. Few direct contacts were observed with Red-tailed Hawks.

Pair 6

Except for a few suburban estates and long-established active farms, this territory was remote. It was outside the city limits. However, there was a new house nearby, and 237 ft (65.5 m) south was a well-traveled gravel road to a resort lake.

Streams in the valley north of the nest were in excellent condition. Until 1973-74, the heavy hemlock-beech forest here was virtually uncut. Small mammals and amphibians were plentiful, but interspecific competition was strong. Barred Owls (*Strix varia*) had been nesting in the same valley; a Sharp-shinned Hawk (*Accipiter striatus*) territory was to the north. Encounters took place with Red-tailed Hawks, Crows (*Corvus brachyrhynchos*), and another pair of Red-shouldered Hawks (no doubt Pair 5, which had its nest 0.5 m [0.8 km] south).

The nest was about 40 ft up in a 25 in (62.5 cm) DBH beech 58 ft (17.5 m) high. The tree stood in a mixed tract of 52 ac (21.1 ha). Trees 3 in and over within the 0.10 ac numbered 37; total basal area was 16.7 sq ft. Ground cover was 35 percent; canopy cover, virtually 100 percent.

Interspecific Competition

Interspecific encounters involving Red-shouldered Hawks were principally with Red-tailed Hawks and Crows. During the 1973 study, two encounters between nesting Red-tailed and Red-shouldered Hawks were noted. In one the single encroaching Red-tailed Hawk was driven off by the female Red-shouldered Hawk. In the other, a single Red-tailed Hawk appeared to pursue a pair of Red-shouldered Hawks. Crows harassed the young of Pairs 1 and 4 and the adults of Pair 3 while we were climbing to their nest. During the latter episode, the Crows seemed dominant through sheer numbers. Crows were also plentiful (perhaps because of nearby garbage) at the site of Pair 4. This pair's nest was also molested by gray squirrels (*Sciurus carolinensis*). The hawks may have moved from nest to nest as a result. Unfortunately no work could be carried out on the relationship between Red-shouldered Hawks and Great Horned Owls. However, during the spring of 1974 these owls occupied the nest of Pair 1 before it returned to the territory. Red-shouldered Hawks were not seen there that year. Owls had not nested within 1.2 mi (1.9 km) in 1972.

Food

No tethering of young below nests for food studies was practicable, we felt, because of the accessibility of the sites.

Despite 12.5 man-hours at each site during the breeding season, I saw only one food transfer between adults. The male of Pair 1 seemed to forage widely, perhaps because of marginal habitat conditions.

Several times Red-shouldered Hawks at study sites were observed perched near singing frogs. Pair 1 was seen to capture a garter snake (*Thamnophis sirtalis*) and a small rodent, which was fed to the young. Icterid or Starling (*Sturnus vulgaris*) bones were found in a pellet below the nest of Pair 3. These animals are known to comprise the main food of breeding Red-shouldered Hawks (Ernst 1945, and others).

Reproductive Performance

Pair 1 produced three young, the only pair of the four with complete data in 1973 to do so. At least two of this brood were fledged (one chick was small and weak, and its fate is unknown). This pair exhibited strong territoriality but were relatively tolerant. Red-shouldered Hawks had occupied this woodlot for at least four years and the same nest for three.

Pair 2 was not seen in the nesting woods after early April. Earlier they had lined a nest and vigorously protested intrusion. Human disturbance, food shortage, and/or successful nesting of Red-tailed Hawks and Great Horned Owls nearby may have caused their disappearance from this apparently new territory.

Pair 3 laid three eggs, one of which was taken for analysis. Two young were ready to fledge in late June. This strongly territorial pair was thought to have nested within a 0.5 mile (0.8 km) radius from at least 1967. Habitat was moderately good but not ideal (i.e., urban).

The outcomes of nestings by Pairs 4 and 5 were not definitely known. Pair 4 was well established but tolerant of disturbance; however, it made three disrupted nesting attempts in 1973. Presumably they finally reared two young, as reported by residents, within the same wooded suburb. Pair 5 was wary but stable; the nest was difficult to observe. Excrement and audible calls led me to believe that young may have hatched. Pair 6 deserted after its clutch of two eggs was taken on 7 May. The nest, apparently a new one and weakly defended, was lined with an abnormal amount of down. Eggs were small and scarcely pigmented. At least one bird remained in the area until August.

Thus, of six nestings studied during 1973 in the Waterloo Region, the outcomes of only four were known definitely. Two clutches of eggs were observed: one with three and one with two. An additional pair, Pair 7, was not studied in detail but was known to fledge one young. Thus from seven nestings, perhaps eight young were reared; seven of these probably fledged (1.0 young fledged per pair). Though my sample size is small, this recruitment rate is not high enough to maintain the population (Henny 1972).

Sixteen nesting records of *B. lineatus* in the Waterloo Region from 1958 to 1972 (Campbell and Royal Ontario Museum, unpublished) fledged an average of 1.7 young each. Ten broods from Royal Ontario Museum data between 1958 and 1961 averaged 2.2 young per brood, which matches other stable populations (Henny 1972). My records for six broods, 1968-72, indicate that the broods averaged only 1.5 young.

Analyses of Eggs

The three eggs collected showed an average decrease of 9.4 percent in shell weight and 11.8 percent in thickness index when compared with pre-1947 figures. Shell thickness averaged 0.311 mm.

Analyses by Ontario Research Foundation for the CWS of the three eggs revealed and following residues, wet weight, ppm: DDE 1.40-3.78; Dieldrin 0.08-0.42; DDD 0.17-0.29; DDT 0.06-0.29; heptachlor epoxide 0.03-0.08; hexachlorobenzene < 0.01; polychlorinated biphenyls 0.87-2.56. Mercury (wet weight) was 0.12-0.34 ppm. The small and poorly pigmented egg from the City of Kitchener (Pair 3) had the highest residue levels for all substances but mercury, which was higher in the rural clutch (two eggs of Pair 6). However, those two eggs, possibly from a young female or a renesting, were also small and poorly pigmented. Compared with three Maryland eggs similarly analyzed (Henny et al., 1973), our sample showed higher levels of all substances except hexachlorobenzene, mercury (not done), and polychlorinated biphenyls. The Maryland eggs came from an extensive, largely forested area.

Discussion and Conclusions

A marked decline has occurred in nesting *B. lineatus* within the study area since the early 1960s. Formerly it was the most common nesting diurnal raptor in the Region. For almost every square mile of favorable habitat, a pair could be found. I knew of six to seven pairs along an 8 mi (13.8 km) stretch of river valley near where Pairs 3 and 4 nested in 1973, and six to nine pairs within a radius of 3.5 mi (5.6 km) of where Pairs 5 and 6 nested in 1973. This decline has been commented upon in other Ontario localities (e.g., Goodwin and Rosche, 1974). A decrease of up to 10 percent (Henny, 1972) has also occurred in parts of the United States. This has also been noted for wintering Red-shouldered Hawks (Brown, 1971) in all States but California and West Virginia. The largest losses seem to be in the Northeast.

The "crash" in Red-shouldered Hawk numbers in Ontario has been dated by Hanna (1973 pers. comm.) and me as beginning about 1964-67. Whether it has continued or has been arrested since 1969 remains uncertain.

Various causes, possibly interrelated in many cases, have been suggested for this decline. One of the most often postulated is habitat change and replacement by the dominant, more xeric-adapted Red-tailed Hawk and Great Horned Owl. The Red-shouldered Hawk prefers fairly sizeable tracts of low, wet woodland, where it often hunts below the canopy. In Waterloo Region most remaining pairs are in river or creek valleys or in swampy bottomlands. Drainage for increased agriculture and urbanization, as well as for deforestation, in southern Ontario has sharply accelerated in recent years. These, a resultant decrease in reptiles and amphibians (important prey for Red-shouldered Hawks), and an increase in mammals favored by Red-tailed Hawks and Great Horned Owls, are undoubtedly important. Notably scarcer here in the breeding seasons before 1958, the Red-tailed Hawk has since reversed its position. Also, like the Great Horned Owl, it breeds earlier than *B. lineatus* and so appropriates its territory.

At Patuxent, Maryland, loss of habitat seems to be the vital factor in a decline of breeding Red-shouldered Hawks. A 9 percent decrease in shell thickness was found between pre-1947 and 1971 in a sample of 15 addled eggs, a value considered too low to impair recruitment (Henny et al., 1973). In Ontario also there has been loss of habitat, but much suitable habitat is now unoccupied. Egg breakage and addled eggs have been reported (Mason, 1971; Frank et al., in press). Eggshell thinning, in addition to the three eggs reported here, has been found in Ontario by Anderson and Hickey (1972), C. A. Campbell (MS report, 1974), and Frank et al. (in press). Values generally have been about the same or slightly higher than the

Patuxent figures but are still below the critical point. Present data, although too few to be definitive, suggest a need for further studies on the possible influence of pesticides on Red-shouldered Hawks in Ontario.

Acknowledgments

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ADOPTION OF NESTLINGS BY BREEDING BALD EAGLES

by

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This paper (1) reports an experiment designed to test whether wild-breeding Bald Eagles (*Haliaeetus leucocephalus*) will accept and raise young other than their own, and (2) discusses possibilities open to the management of this declining species.

That breeding raptors will accept and raise nestlings not their own is well known. Postupalsky has moved "runt" Osprey (*Pandion haliaetus*) chicks from large broods to be raised in other active nests of the same species. Holt has done this routinely with Red-tailed Hawks (*Buteo jamaicensis*) and once with the Great Horned Owl (*Bubo virginianus*) in his study area in southwestern Ohio. Olendorff and Stoddart (1974) mention similar fostering of Ferruginous Hawks (*Buteo regalis*) and Golden Eagles (*Aquila chrysaetos*). In Europe, Meyburg (1971) and Meyburg and Heydt (1973) have used this technique to increase nestling survival in the Spanish Imperial Eagle (*Aquila heliaca*) and the Lesser Spotted Eagle (*Aquila pomarina*). Chicks of the latter were raised by foster parents of different species—Black Kites (*Milvus migrans*) and Common Buzzards (*Buteo buteo*). Stohn (1974) reports a successful adoption of a Common Buzzard nestling by a pair of Goshawks (*Accipiter gentilis*) that raised it along with their own single young.

This brief review is by no means exhaustive. In view of experience with other raptors, we did not expect that Bald Eagles would react differently under similar circumstances. However, to our knowledge, no comparable experiments have ever been attempted with this species.

On 16 June 1974 two young Bald Eagles were found on the ground near Loud Dam Pond on the Au Sable River in Iosco County, Michigan, the day after a severe storm had destroyed the nest. These were the eaglets that Holt had banded there on 9 June when they were 7½ to 8 weeks old. The birds were turned over to the Michigan Department of Natural Resources (DNR) and the U. S. Fish and Wildlife Service (USFWS) and were eventually placed in the Kellogg Biological Station and Bird Sanctuary near Battle Creek. They were then about 9 weeks old and would be able to fly in another week or two. As the eaglets were apparently healthy and uninjured, we decided to place them in two nests, each containing a single eaglet of similar size and age. We knew of one such suitable nest in an oak near Fairview in Oscoda County and one of another in a white pine near Atlanta in Montmorency County. Both nest sites are well protected on private hunting clubs, each with a resident caretaker.

In the meantime, Federal agents "repossessed" the two eaglets and brought them to Lansing. Both birds refused to eat at first. We force-fed them a few times, after which they readily accepted food (thawed, beheaded smelt) from our hands.

We departed from Lansing early on 20 June with each eaglet in a large box. The caretakers of both properties readily granted permission to place the young eaglets in the

selected nests. The larger eaglet, a female, was placed in the eyrie near Fairview with a female eaglet already present. A supply of smelt was left near the edge of the nest. One adult was circling overhead during the transfer. Upon returning to the nest about one-half hour later, we noted that both young were standing on the nest, about 2 feet apart, showing no overt signs of aggression. Later the same day we placed the male eaglet and some smelt in the eyrie near Atlanta. One adult was flying overhead when we arrived but disappeared from view later. While Holt was at the nest, the native eaglet, believed to be a female, moved out on a branch. As we left the site, the transplanted eaglet was standing in the nest and the native bird was perched on the limb about 3 feet from the rim of the nest.

Michigan DNR pilot Frank Bennett saw both eaglets on a branch next to the Atlanta nest on 27 June, 1 week after the transfer. On 24 July, while flying a survey of Osprey nests in the area, Postupalsky checked this site again. As the plane approached, two large juvenile eagles flew from the nest tree and headed toward another pine nearby.

At the Fairview site both eaglets were on the nest on 26 June when U.S. Forest Service biologists G. W. Irvine and Craig Orr flew over. On 6 July Orr found both eaglets standing on the edge of the nest, appearing "vocal, very healthy, and vigorous." One finally flew a short distance, while the other remained on the nest. On 14 July Orr saw both young take flight from the eyrie and return to it a short time later. On 16 July he found the nest empty, but both young eagles returned and landed on it while he was watching.

Follow-up observations indicate that the transfer of nestlings was successful. All four young fledged. Breeding Bald Eagles, like many other raptor species, will adopt and raise extra nestlings. It further supports the view that raptors, in contrast to colonial breeders, such as gulls, have not evolved an ability to recognize their own offspring. Under natural conditions nestling raptors do not normally find themselves in "strange" nests; therefore, no selective pressure exists in this group to favor development of parental ability to recognize their own young. Breeding raptors thus respond to any nestling in "their" nests.

The fostering technique has definite potentialities in Bald Eagle management. (1) Nestlings that survive the crash of a nest uninjured can be placed in other active nests and thus remain part of the wild population. Such transfers should be possible where banders are active and familiar with most nests, their contents, and ages of young present. About 90 percent of the known annual production of Bald Eagles in Michigan and Wisconsin are now being banded. (2) The technique opens the possibility of using nestlings from healthy populations to bolster threatened populations, such as those in Maine or near Lake Erie. (3) Banders finding broods of three young could assist in transferring the third nestling to eyries in other areas. Although a high proportion of pairs in the Great Lakes States produce 3-egg clutches, fewer than 5 percent raise broods of three to fledging age (Grewe, 1966; Sprunt *et al.*, 1973; Postupalsky, unpubl.). (4) Nestlings produced in captivity may likewise be fostered in active eyries in the wild.

We gratefully acknowledge assistance of several persons without which the transfer experiment would not have been possible: T. V. Heatley and M. Stanek assisted in the field; R. H. Morman, W. Fuchs, and T. V. Havard supplied information on the circumstances of the eaglets' capture; J. G. Sieh secured the necessary permission from the USFWS Regional Director and helped in other ways; and G. W. Irvine, C. Orr, R. G. Strong, and F. Bennett supplied notes on follow-up observations. The experiment was conducted while Postupalsky was employed by the USFWS. Our banding work was made possible by travel funds from Conservation for Survival.

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A PLEA FOR INFORMATION

A study is currently in progress to determine the historical and present status of the Great Gray Owl (*Strix nebulosa*) in North America. Any information regarding sight records or possible breeding occurrences of the Great Gray Owl is urgently required. Your cooperation will be gratefully acknowledged.

Please write to: M. Collins
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NEED INFERTILE EGGS

We are currently studying egg shell characteristics and gas exchange across egg shells of various species of birds. We have found that from these studies we can determine water loss from the egg and approximately calculate incubation times. We can also draw conclusions as to requirements for incubation, including optimal humidity. These studies can be performed with infertile eggs. Accordingly, we would be grateful if those who breed raptors and have infertile eggs would send us these eggs, well wrapped against breakage. We can pick up eggs from raptor breeders located not too far from our laboratories. Please contact Julian L. Ambrus, M.D., Ph.D., Springville Laboratories, Roswell Park Memorial Institute, State of New York Department of Health, 571 East Main Street, Springville, New York 14141 (716-592-2834 or 716-592-3101).

THE ROLE OF VACCINATION IN THE MAINTENANCE OF CAPTIVE BIRDS OF PREY

by

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ABSTRACT. The diseases of raptors against which vaccination is or could be practicable are discussed. Particular mention is made of Newcastle disease and agian pox. Other diseases discussed in the context of vaccination are pasteurellosis, salmonellosis, tuberculosis,umblefoot, aspergillosis, Marek's disease, and inclusion body hepatitis. The need for more research on this topic is emphasized.

Introduction

There has been great interest in the breeding of captive birds of prey in the past five years. As a result, the numbers of birds maintained in captivity have increased, and there has been a marked awareness of the potential dangers of disease.

Despite great advances in hawk medicine in the last decade, many diseases remain a threat to captive raptors. The relatively intensive systems used for captive breeding increases the risks of epizootic disease and build-up of parasites. Prophylactic vaccination has proved invaluable in the prevention of epizootic disease in intensively reared poultry and could possibly be of use in captive raptors (Cooper 1972a). However, little work has been carried out on this topic.

In this paper I discuss raptor diseases against which vaccination might be practicable. Where appropriate, results and conclusions are recorded. Clinical signs and other features of the diseases are not given; these data are available elsewhere (Hofstad et al., 1972; Davis et al., 1971).

Materials and Methods

The birds I vaccinated were captives maintained at the Veterinary Research Laboratory, Kabete, Kenya, East Africa (Table 1). Techniques of vaccination are discussed under each disease.

Results and Discussion

Newcastle Disease. This viral disease is a definite threat to birds of prey, having been reported on a number of occasions from a variety of species (Keymer and Dawson, 1971; Schoop et al., 1955; Zuydam, 1952). As with other such diseases, there is no specific treatment; control in domestic birds rests upon prophylactic vaccination with either killed (inactivated) or living (attenuated) vaccines.

The various types of Newcastle vaccine were discussed by Lancaster (1966). Vaccination of raptors with an inactivated Newcastle disease (ND) vaccine (Cooper, 1972a) and with an attenuated vaccine (Hornbuckle 1972) have been reported. However, while reporting the safety of the vaccine used, these authors made no mention of the efficacy of vaccination either in terms of immunogenicity or protection.

Subsequently, I had the opportunity to carry out a small number of trials with inactivated Newcastle disease vaccination of raptors in Kenya. The vaccine was a B-propiolactone vaccine prepared in embryonated hens' eggs, a technique used extensively to immunize poultry in Kenya. Injection was subcutaneous, usually over the pectoral muscle or leg, at a dosage of 1.0 ml. To test for safety of the product, the birds received a clinical examination daily, and the site of inoculation was palpated and observed. The birds showed no generalized or localized ill effects other than slight swelling and, in some cases, caseation at the site of vaccination.

Later, the serological response to the vaccine was studied. It was impracticable to challenge vaccinated birds; therefore, the haemagglutination inhibition (HAI) titre to the virus was used as an indicator of immune status. This test has been used extensively in work with poultry in which the HAI titre is believed to correlate closely with protection. In the raptor work, blood samples were taken from the brachial vein at the time of vaccination and at weekly (or in some cases twice-weekly) intervals for six weeks. At least 1.0 ml of blood was taken from each bird and allowed to clot. The resulting serum was used for an HAI test using avian red blood cells and a Newcastle disease virus of known HAI titre.

A very poor response to Newcastle vaccine resulted. The majority of birds either showed a negative titre prior to vaccination or a low titre of 1/10 or 1/20. Following one dose of vaccine the titre rose in approximately 50 percent of cases, but the majority of these showed only a one or two cell difference (e.g., from 1/10 to 1/20 or 1/40). This was not considered significant. The highest titre reached was 1/160, 3 weeks after vaccination of a Tawny Eagle which initially had a titre of 1/20. Even this titre returned to 1/80 in the fourth week and thereafter remained constant.

Subsequent doses of vaccine were given to the Tawny Eagle at varying intervals following the first injection. On no occasion was a significant rise in titre observed.

To check the efficacy of the vaccine in poultry, samples were also inoculated into three-week-old chickens; similar serological tests were performed. The results contrasted markedly with those in the raptors. There was a rise in titre after two weeks, in some cases to 1/1280 or 1/2560. Subsequent vaccination produced a further rise in titre.

The results in raptors are disappointing and suggest that these birds respond poorly to a β -propiolactone inactivated vaccine. Such a response is well documented in the turkey (Box et al., 1974) and poses problems when this species must be vaccinated. Unfortunately other types of Newcastle disease vaccine are not used in Kenya; further trials could not be performed. A recent report (Chew and Liow, 1974) describes the successful use of live vaccines in psittacine birds. Work on these vaccines in raptors would appear warranted.

Avian Pox. This disease has been reported in raptors on a number of occasions (e.g., Cooper, 1969; Greenwood and Blakemore, 1973). It is probably only rarely fatal but can produce severe clinical signs which may render a hawk unable to feed or otherwise incapacitate it. Certainly avian pox is a potential hazard to captive raptors. In the absence of any specific therapy, vaccination is desirable.

I have found no reports on the use of a pox vaccine in raptors or in other wild birds. However, considerable work has been performed on the vaccination of poultry and other domestic birds, including pheasants (Dobson 1937). The subject is also discussed by Cun-

ningham (1965). However, as Karstad (in Davis et al., 1971) points out, careful consideration must be made of the strain involved, since avian pox viruses show variation in pathogenicity for different species.

I used an attenuated pox vaccine on a Tawny Eagle in Kenya. The vaccine, a pigeon-pox-derived strain, was given by wing stab; 0.1 ml was also injected subcutaneously in the same area. Despite daily examinations, no systemic or local effects were noted. Similar negative results were shown by a Marabou Stork (*Leptoptilos crumeniferus*) inoculated by the same route. Poultry vaccinated by wing stab alone developed a small pustule at the site 5 to 10 days later.

Pasteurellosis (Avian Cholera). This disease has been observed among a number of raptors, both captive and free living, and is discussed in detail by Rosen (in Davis et al., 1971). Free-living birds may contract the infection by feeding upon infected birds or rodents (Rosen and Morse, 1959).

Although treatment of pasteurellosis is possible, the disease is often peracute or acute, and success rates may be low. Vaccination against pasteurellosis is of some historical interest because Pasteur (1880a, 1880b) performed his early immunological experiments with this disease and succeeded in protecting a percentage of chickens with an attenuated strain of the organism. Much work has followed, and both attenuated and inactivated vaccines have been developed, but I have found no record of their use in raptors.

An inactivated *Pasteurella multocida* vaccine was used in three species: Tawny Eagle, African Hawk Eagle, and Black Kite. Again no attempt was made to assess its efficacy, but the birds were observed carefully for systemic or local side effects. None was noted. The dose used was 1.0 ml subcutaneously. No poultry were vaccinated, but the vaccine used is the standard vaccine for poultry in Kenya.

Salmonellosis (Avian Typhoid). Salmonellosis has been reported from a number of raptors but usually only in isolated cases. A recent publication from Hanover (Tabken, 1972) discusses salmonellosis in the context of the conservation of Peregrines. Tabken collates a formidable list of *Salmonella* spp. identified in nest material, castings, and feces from Peregrine eyries. Under the intensive conditions of captive breeding, a *Salmonella* sp. could prove an important hazard. Prophylactic vaccination would seem advantageous.

Numerous attempts have been made to produce a *Salmonella* vaccine for birds but with very little success, despite the production of an attenuated *S. dublin* vaccine for cattle. A killed vaccine against *S. gallinarum* was used to inject a Tawny Eagle, an African Hawk Eagle, and a Black Kite in Kenya. The poultry dose of 1.0 ml was given subcutaneously. No ill effects were noted.

Avian Tuberculosis. This condition occurs in both captive and free-living raptors. The causal organism is relatively resistant to disinfectants and this, coupled with the difficulties of clinical diagnosis, make contamination of aviaries or mews a real hazard.

Vaccination of poultry has been attempted with slight success, but it is usually not recommended. Viza, Douza, and Pasztor (1964) reported 100 percent success with a killed vaccine in a zoological collection, but no other reports have been traced. Dr. A. McDiarmid of the Institute for Research on Animal Disease, Compton, Berkshire (pers. comm.), reports investigations into the use of BCG as a vaccine in pheasants, waterfowl, and poultry. There is "some evidence to indicate that BCG may be of value." It does not yet appear to have been used in birds of prey.

Bumblefoot. This condition is an important clinical condition of captive raptors. While treatment by medical or surgical means is frequently successful, prevention is preferable. The condition is usually associated with bacteria, especially *Staphylococcus aureus*, and it has

been postulated (Cooper, 1972a) that immunization might prove of value in prevention and treatment.

Staphylococcal toxoid (Burroughs Wellcome & Co.) has been administered by intramuscular injection to both Lanners and Peregrines suffering from bumblefoot, but no obvious value has been noted. No attempt has yet been made to use this toxoid prophylactically. It is my opinion that an autogenous vaccine, prepared from the causal organism, might prove more valuable. However, organisms other than *S. aureus* can also be associated with bumblefoot. Control of this one bacterium will not necessarily, therefore, ensure protection against the disease. Moreover, other factors such as overgrown talons and poorly designed perches predispose raptors to bumblefoot; attention to these aspects may prove of more practical value in disease prevention.

Aspergillosis. This is a common cause of death in captive hawks and frequently supervenes following such factors as loss of condition and intercurrent disease.

Vaccination against aspergillosis has been suggested previously (Cooper, 1972b), following experimental work with mice reported by workers in England. Little is known of the immunological aspects of *A. fumigatus* infection, but the limited work performed to date would suggest that vaccination might prove of value.

Marek's Disease. Marek's disease apparently is not a problem in raptors, though isolated cases have been reported (Halliwell, 1971; Woodford and Glasier, 1955). I mention the possibility of vaccination because of the successful development of attenuated vaccines for poultry. The disease could conceivably prove more of a threat now that captive breeding is widely attempted. An example of an instance when a suitably safe Marek's vaccine might have proved valuable was Dr. Stanley Temple's work with the Mauritius Kestrel (*Falco punctatus*). Marek's disease is enzootic on Mauritius; and Dr. Temple, who fed chicks to his captive pair of Kestrels, feared that the latter might become infected. It appears, however, that the disease is probably not a great threat to raptors, and incubator-hatched day-old chicks are unlikely to carry infection.

No records have been traced of the use of poultry vaccines in birds of prey, and I would not advocate their use until experimental work has shown them to be safe.

Inclusion Body Hepatitis. To date, this disease has been observed only among falcons in the United States of America (Ward, Fairchild, and Vuicich, 1971; Mare and Graham, 1973), but it has attracted considerable interest in all countries where raptors are maintained in captivity. A similar disease is known from owls in Europe (Burtscher, 1968; Burtscher and Schumacher, 1966).

Protection of birds against inclusion body hepatitis would be of considerable potential value, but production of a vaccine would seem unlikely because the causal agent is a herpes virus. Such viruses frequently persist in the presence of circulating antibodies. However, as Mare and Graham (1973) point out, the virus may not be as cell associated as are some other herpes viruses. This could facilitate development of a vaccine.

Conclusions

There have been few attempts to vaccinate birds of prey against disease, and relatively little is known of their immunological response to microorganisms. My limited work with inactivated Newcastle disease vaccine suggests that the raptor's immunological response to this vaccine may not follow that of the fowl.

There have been great advances in the development and improvement of poultry vaccines in the past five years. Increased interest in the maintenance of hawks in aviaries suggests that research on the development of vaccines for these birds may be long overdue.

Acknowledgments

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TABLE I

SPECIES IN WHICH VACCINES USED

1. Tawny Eagle (*Aquila rapax*) NDV P PS S
2. African Hawk Eagle (*Hieraaetus fasciatus*) NDV PS S
3. African Harrier Hawk (*Polyboroides typus*) NDV
4. African Goshawk (*Accipiter tachiro*) NDV
5. Black Kite (*Milvus migrans*) NDV PS S
6. Augur Buzzard (*Buteo rufofuscus*) NDV
7. Lanner (*Falco biarmicus*) NDV ST
8. Peregrine (*F. peregrinus*) NDV ST
9. White-backed Vulture (*Gyps africanus*) NDV
10. Hooded Vulture (*Necrosyrtes monachus*) NDV
11. Spotted Eagle Owl (*Bubo africanus*) NDV
12. Barn Owl (*Tyto alba*) NDV

Key NDV = Newcastle
S = Salmonellosis

P = Pox PS = Pasteurellosis
ST = Staphylococcal toxoid

BIBLIOGRAPHY ON THE PEREGRINE FALCON

The U.S. Fish and Wildlife Service is compiling a bibliography with abstracts of English language literature, both books and periodicals, on the Peregrine Falcon (*Falco peregrinus*). Authors who wish to have their articles included in this work should send two reprints, copies, or abstracts to the senior author, Dr. Richard D. Porter, I.F. & R.E.S. Shrub Lab, 735 North 500 East, Provo, Utah 84601.

Articles in which the Peregrine Falcon is mentioned but is not the main subject, and articles in foreign languages with English summaries are also wanted.

A MORPHOLOGICAL COMPARISON OF TWO HARRIER POPULATIONS

by

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Introduction

Harriers have been studied intensively in two separate study areas: *Circus c. cyaneus* in Orkney, Scotland, latitude 59° N (Balfour, 1957, 1962, 1970; Scharf, 1968; and Scharf and Balfour, 1971) and *C. c. hudsonius* in central Wisconsin, latitude 43° N (Hamerstrom, 1963, 1968, 1969; Hamerstrom and Wilde, 1973, and Schmutz and Schmutz, 1975). Both populations are migratory, but both were studied during the breeding season, which provided an excellent opportunity for comparison of two geographically separate breeding populations (demes). Comparisons were not made with findings in the existing literature since the latter have dealt with composites of breeding, migrating, and wintering birds.

In all, 284 birds were weighed, measured, and otherwise examined during the course of banding: Scharf and Balfour trapped 55 breeding hen harriers near 54 nests during 1967 and 1968; Hamerstrom and co-workers trapped 130 breeding American harriers near 139 nests from 1960 to 1972; and a separate sample of 99 Wisconsin migrants was handled. Our sample size varies because occasionally we failed to take a measurement.

Plumage

Differences in plumage are not great, but are consistent within each population. The bars on the tail of adult male *cyaneus* are paler than those of *hudsonius*, and the female's plumage is browner, both dorsally and ventrally.

Wing Length

At first we included migrants in our Wisconsin sample. We were puzzled to find that migrant adult males and females alike had slightly longer wings than the breeders. The migrants were all trapped in spring, for the most part in April, and most of the breeding birds were trapped about three months later—usually in July. We attribute the difference to feather wear. It may also be true that individuals of the central Wisconsin deme were slightly smaller than those passing through the area.

In either case it seems best to limit our comparisons to the breeding populations. For these samples we used trapping methods which were essentially comparable in the two areas and which were specific for breeders. All harriers were caught while defending their nests against an owl (Hamerstrom, 1963; and Scharf, 1968), with the exception of 10 miscellaneous catches, also known to be breeders. Furthermore, we have excluded breeding juveniles, using Hamerstrom's (1968) criteria.

Our technique for measuring the flattened wing was to strive for the maximum measurement. We placed the folded wing parallel to the rule and stretched it from the tip of the longest primary to the bend of the wing, simultaneously pressing on the distal end of the metacarpal to bring the phalanges parallel to the rule; meanwhile the wing was pressed flat to get rid of the curvature of the primaries. On birds larger than Kestrels (*Falco sparverius*), this measurement is more easily taken by two people. When working alone we held the tips of

the primaries in position on the rule with our toes. Chords were measured in the usual manner: the folded wing was placed on the rule to allow for the natural curvature of the feathers.

It is important, we believe, to mention that we were aware of the need to standardize our measuring technique. During the summer of 1964 Scharf and Hamerstrom worked together in the field on these measurements, and each in turn taught his co-workers to measure in the same manner.

Measurements of wing length for both populations are shown in table 1. Within each population there is an obvious difference in wing length between the sexes. But within each sex, there is only a small standard deviation on either side of the mean, indicating a high degree of homogeneity within each deme (figure 1). Between Orkney and Wisconsin populations, moreover, there is a significant difference in wing length. Orkney males average 19.0 mm shorter (flattened) than Wisconsin males, and Orkney females average 20.6 mm shorter than those captured in Wisconsin. The corresponding chord measurements showed Orkney males 14.4 mm shorter and Orkney females 15.4 mm shorter.

It has been difficult in the past to compare the wing lengths of *cyaneus* and *hudsonius* on a continental basis because Europeans tend to measure the flattened wing (Witherby et al., 1943) and Americans the chord (Friedmann, 1950). We plotted flattened lengths against chord lengths for our *cyaneus* and *hudsonius* populations (figure 2). We find the figure useful for conversion if one has only one type of measurement and seeks the other. The proportionate ratio of flattened to chord in figure 2 may not hold true for dried museum skins where the dimensions may have changed—i.e., the upper wing shrinks or becomes less flexible in the dried skin, hence the length is reduced (Mueller and Berger, 1968). The straight-line relationship in figure 2 can be calculated from linear regressions. Significance tests show that mean corrections would be less than 1 mm at the 95 percent confidence level. This implies that groups of 50 or more measurements would lie within 1 mm of the respective converted chord of flat length.

Weight

The Orkney birds were weighed on Pesola spring scales; a beam balance was used in Wisconsin. Because nearly all birds were trapped when defending their nests, almost none had food in the crop. We therefore made no correction for possible crop contents. Weights are given in table 2 for comparison.

We found so much variation in both Wisconsin and Orkney weights that they do not seem particularly useful for comparison. Our differences in means are not statistically significant ($p > .05$). Although our samples were all taken during the breeding season, there was considerable year-to-year variation in mean weights of both sexes: Wisconsin females ranged 70 g (from 481 to 551 g) and males 43 g (from 305 to 348 g). In Orkney, females ranged 16 g (from 510 to 526 g) and males 19 g (from 337 to 356 g).

Egg Color

Balfour (1962) stated that the eggs of harriers in Orkney are blue when laid and turn white in about a week or less. Hamerstrom (1969) found that *hudsonius* eggs also turn from blue to white, but 2-3 days after laying. We suspect that eggs bleach more quickly under sunny Wisconsin skies than on the misty moors of Orkney.

Eye color

Young female harriers have chocolate-brown irises that change to yellow with age.

Judging the percent of brown in the iris is subjective, but Scharf and Hamerstrom examined live birds together and with their co-workers to standardize their evaluations. In addition, Scharf maintains a series of color transparencies of the Orkney birds for reference.

The rate of change, however, is not the same. Orkney female harriers retain their dark iris color longer than those in Wisconsin. Hamerstrom (1968) showed that only first-year females had irises that were more than 50 percent brown. (In 1970 she trapped an exception: a brown-eyed female, aged 2). Two of her three second-year Wisconsin females had attained irises that were almost wholly yellow. Balfour (1970) reported the brown irises retained through ages 3 to 4 years, and Scharf has record of one known-age Orkney female of 5 years with a brown iris.

It at first appeared that the age composition of the two populations was similar, on the basis of eye color of the trapped sample. In Orkney, 53.4 percent of the nesting females trapped had brown irises; in Wisconsin the figure was 58 percent. However, some of the Orkney brown-eyed individuals were as old as 5 years, whereas only one of the Wisconsin females with brown irises was over one year old. This striking difference in actual age composition of the two populations is an example of the care that must be exercised in using eye color in population studies.

Summary and Conclusions

We compared wing lengths, weights, egg color, and eye color of two harrier populations: *Circus cyaneus hudsonius* in central Wisconsin and *C. c. cyaneus* in Orkney, Scotland. As the wings of Wisconsin adults during the breeding season average slightly shorter than those of spring migrants (we suspect feather wear), we base our comparisons on adults during the breeding season. Each deme is remarkably homogeneous for the parameters studied, except for weights. Wing lengths differed significantly between sexes and demes. We suspect that Orkney eggs hold their blue color longer, but further field work needs to be done. Irises of Orkney females tend to turn yellow later in life than those of Wisconsin females.

We show that a significant difference exists between chord and flattened-wing measurements and have presented a practical method of comparing chord and flattened wing, making it possible to compare measurements as given in the literature.

Considering only our comparisons, the suggestion by Brown and Amadon (1968, Vol. 1, p. 392) that the two forms from Eurasia and North America may be distinct species seems to be warranted.

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Table 1. Comparison of adult breeding harriers in Orkney and Wisconsin: flattened wing versus chord (in mm).

	Flattened			Chord		
Male	N	Range	Mean	N	Range	Mean
<i>hudsonius</i>	39	334-370	(351.3)	38	325-361	(341.4)
<i>cyaneus</i>	12	322-340	(332.3)	14	316-335	(327.0)
Female						
<i>hudsonius</i>	66	376-416	(393.7)	66	361-409	(382.0)
<i>cyaneus</i>	36	358-384	(373.1)	39	357-379	(366.6)

Orkney measurements are significantly shorter than Wisconsin: males, $t=7.72$, 49 df, $p < .01$; females, $t=11.8$, 100 df, $p < .01$.

Table 2. Comparison of adult breeding harrier weights (in g): Orkney and Wisconsin.

	Male			Female		
	N	Range	Mean	N	Range	Mean
<i>cyaneus</i>	15	298-372	(367.4)	42	473-595	(529.9)
<i>hudsonius</i>	44	304-363	(334.0)	61	463-591	(515.8)

Differences are not significant ($p > .05$).

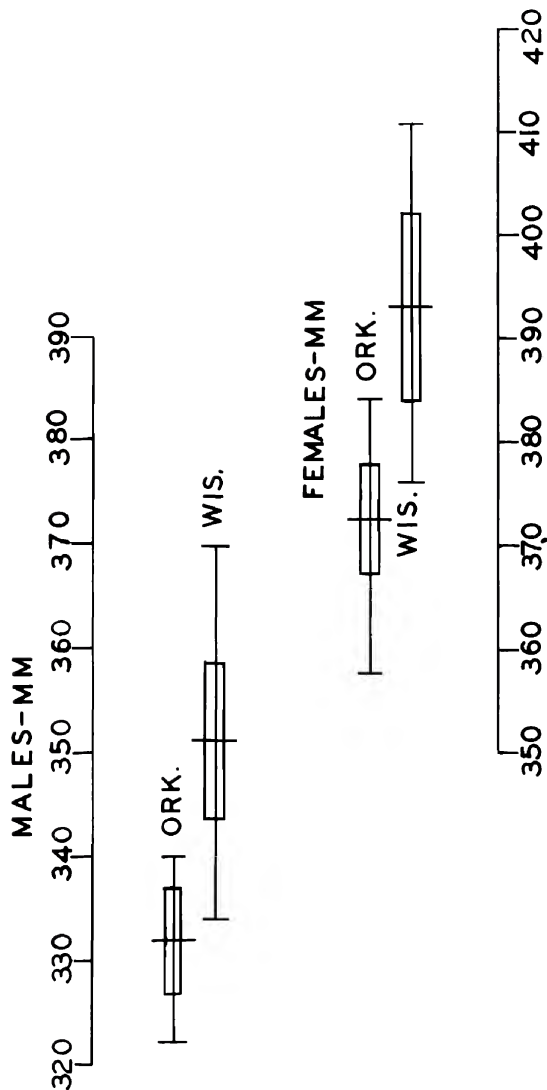


Figure 1. Flattened wing lengths, by sex, of two breeding adult harrier populations. Vertical bars indicate range and mean; blocks indicate ± 1 S.D. Orkney measurements are significantly shorter than Wisconsin: males, $t=7.72$, 49 df, $p<.01$; females, $t=11.8$, 100 df, $p<.01$.

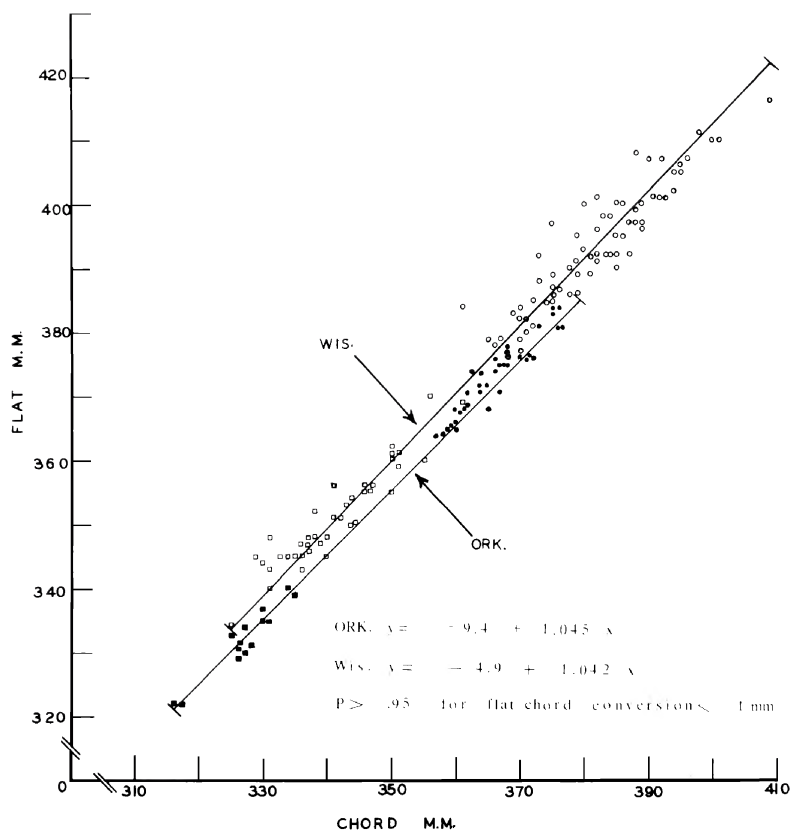


Figure 2. Comparison of flattened and chord measurements of wings of breeding adults of two harrier populations. Solid squares represent Orkney males; dots, Orkney females. Open squares represent Wisconsin males; circles, Wisconsin females. Lines represent regression calculation using extremes of X (bar) to calculate Y for each population. Difference between regressions not significant $p > .05$.

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